

## ARTICLE

# Coexistence in an African pastoral landscape: Evidence that livestock and wildlife temporally partition water resources

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## Abstract

African rangelands support substantial wildlife populations alongside pastoralists and livestock. Recent wildlife declines are often attributed to competition with livestock over water and grazing, in part because livestock are thought to spatially displace wildlife. However, more evidence is needed to understand this interaction and inform rangeland management. Here, we analysed the temporal overlap between wildlife and livestock at water points in a community-governed area of Kenya's South Rift Valley, which is a dry season refuge where Maasai pastoralists, livestock and wildlife co-occur. We used camera traps to capture images at water points in two time periods: first, when nearby settlements were unoccupied, and second, as people and their herds moved into the area. We measured wildlife activity (independent detections per hour) and the difference in temporal overlap between livestock and wildlife. We found no evidence that daily wildlife activity declined despite increased human and livestock settlement. However, temporal partitioning between livestock and wildlife at watering points increased with wildlife using water resources more at night. Maasai corral livestock overnight to protect them from predation, allowing wildlife to persist in a livestock-dominated landscape. Our study demonstrates humans and wildlife co-adapting to mitigate competition for shared water resources, thereby facilitating spatial coexistence.

## KEYWORDS

coexistence, Kenya, livestock, pastoralism, water points, wildlife

## Résumé

Les pâturages africains abritent d'importantes populations d'animaux sauvages en plus des pasteurs et du bétail. Les déclinés récents de la faune sont souvent attribués à la concurrence avec le bétail relative à l'eau et aux pâturages, en partie parce qu'il est présumé que le bétail déplace la faune dans l'espace. Cependant, des preuves supplémentaires sont nécessaires pour comprendre cette interaction et éclairer la gestion des pâturages. Dans cette étude, nous avons analysé le chevauchement temporel entre la faune et le bétail aux points d'eau dans une zone communautaire de la vallée du Rift

Sud, au Kenya, qui est un refuge en saison sèche où cohabitent pasteurs Massaïs, bétail et faune. Nous avons utilisé des pièges photographiques pour capturer des images aux points d'eau sur deux périodes; d'abord, lorsque les points d'implantation voisins étaient inoccupées, et ensuite lorsque les gens et leurs troupeaux se sont installés dans la région. Nous avons mesuré l'activité de la faune (détections indépendantes par heure) et la différence de chevauchement temporel entre le bétail et la faune. Nous n'avons trouvé aucune preuve que l'activité quotidienne de la faune diminuait malgré l'augmentation des établissements humains et du bétail. Cependant, la répartition temporelle entre le bétail et la faune aux points d'eau a augmenté, la faune utilisant davantage les ressources en eau la nuit. Les Massaïs enferment le bétail dans des enclos pendant la nuit pour les protéger contre les prédateurs, ce qui permet à la faune de persister dans un paysage dominé par le bétail. Notre étude démontre que les humains et la faune s'adaptent mutuellement pour atténuer la concurrence relative aux ressources en eau partagées, facilitant ainsi la coexistence spatiale.

## 1 | INTRODUCTION

Rangelands worldwide hold immense economic and social importance, providing food security for millions of people and supporting their livelihoods (Lund, 2007). Rangelands are 'areas where wild and domestic animals graze or browse on uncultivated vegetation' (Food & Agriculture Organization, 2000) and predominantly occur in the grassland, savannah and shrubland biomes (Olson et al., 2001), covering approximately 54% of terrestrial ecosystems (Sala et al., 2017). They provide vital ecosystem services including carbon sequestration, forage and soil conservation (Lund, 2007; Sala et al., 2017). In particular, rangelands are essential for subsistence pastoralists and their livestock, sustaining 30% of the world's population (Sala et al., 2017). African rangelands support the largest large mammal populations on the planet, including several of the last great migrations (du Toit et al., 2010). Examples include the 1.3 million wildebeest (*Connochaetes taurinus*) in the Serengeti-Mara ecosystem, in Tanzania and Kenya (Serneels & Lambin, 2001), and the 800,000 white-eared kob (*Kobus kob leucotis*) in South Sudan (Marjan, 2014).

Protected areas are the primary tool for conserving African wildlife. However, protected areas across Africa's rangelands are too small to halt all species declines and avert extinctions (Larsen et al., 2015; Aichi Targets, 2018). For example, in Kenya, protected areas provide adequate protection for less than half of all amphibians, birds and mammals (Tyrrell et al., 2019), and large wildlife populations exist beyond the boundaries of government-run protected areas (Ogutu et al., 2016; Western et al., 2009). Moreover, many protected areas fail to cover entire functional ecosystems that include both wet and dry season resources, which are important for the productivity and resilience of wildlife populations (Beale et al., 2013; Fynn & Bonyongo, 2011). Community lands beyond protected areas are therefore of great importance for conservation (Western et al.,

2015). Encouragingly, community and private wildlife conservation initiatives have seen notable growth since the 1990 s (Glew et al., 2010; Western et al., 2015) and are increasingly being recognised as 'other effective area-based conservation measures' (OECMS) for their contributions to conservation (Dudley et al., 2018). Kenya is a good example, boasting 160 private and community-based conservancies, covering over six million hectares of rangeland in 28 counties (KWCA, 2019). These conservancies harbour wildlife, people and their livestock.

Historically, large populations of livestock and wildlife have co-occurred in Kenyan rangelands, but wildlife numbers have declined by 40–70% in the last 40 years due to increasing human pressure (Ogutu et al., 2016), mirroring declines across Africa (Craigie et al., 2010). These declines highlight the need for human–wildlife coexistence in shared rangelands. Coexistence can be defined as a sustainable state of cohabitation between wildlife and people in a shared landscape (Carter & Linnell, 2016; Western, 2018). To coexist, both people and wildlife must adapt to living in the same ecosystem, sharing space and time (Carter & Linnell, 2016). Additionally, coexistence with wildlife usually requires a level of cultural tolerance (Western, 2018).

Coexistence is a trade-off between costs and benefits. Traditionally, the relationship between wildlife and livestock in Africa has been viewed as antagonistic (Ogutu et al., 2011), with wildlife posing both direct and indirect costs to people and their herds. Direct costs include competition between livestock and wildlife for grazing and water, and disease transmission (Kock et al., 2009; Odadi et al., 2011). Conflict with predators and dangerous herbivores (e.g. cape buffalo [*Syncerus caffer*]) also creates direct costs, such as livestock depredation, crop loss, and human injuries and fatalities (Chaminuka et al., 2012; Zimmermann et al., 2009), and indirect costs, including opportunity costs from time lost guarding crops or livestock, and detrimental mental and physical health effects (Barua et al., 2013).

Nevertheless, these potential costs of livestock–wildlife coexistence have to be considered against the ecological and economic benefits of coexistence. Ecological benefits of coexistence include increased availability of high-quality, nutrient-rich grazing and reduced tick abundance (Fynn et al., 2016; Keesing et al., 2018), as well as improved forage quality for cattle in the wet season, when livestock and wildlife compete for forage in the dry season (Odadi et al., 2011). The economic benefits of coexisting with wildlife are most apparent where eco-tourism provides a substantial additional revenue stream for pastoralists, such as in the conservancies around the Maasai Mara and in Laikipia, in Kenya (Keesing et al., 2018). Since livestock are now the dominant ecological force across most rangelands (du Toit & Cumming, 1999; Hempson et al., 2017), understanding coexistence between people, livestock and wildlife is critical for conservation.

An ideal location to study coexistence between livestock and wildlife is in the Shompole and Olkiramatian group ranches of Kenya's South Rift Valley—a place where Maasai and their livestock live with a nearly complete assemblage of herbivore and carnivore species (Schuette et al., 2013). Maasai livelihoods are largely reliant on livestock; they maintain a transhumant pastoralist lifestyle, involving seasonal movement of livestock between established areas to find the best grazing available (Western, 2018). As they migrate throughout the year, Maasai herders house their livestock in permanent and temporary bomas. A boma is a 'circular corral of thorn bush designed to protect human and livestock occupants' (Western & Dunne, 1979). Livestock are actively herded during the day, then corralled nightly in bomas to protect them from predation and theft. It is possible that corralling livestock overnight facilitates coexistence and allows wildlife to access shared water and grazing resources at night; however, to the best of our knowledge, no studies have quantified this (Tyrrell et al., 2017).

Livestock and wildlife also potentially compete over water resources (Bourn & Blench, 1999). Water is important in determining distributions of wildlife and livestock (Mizutani et al., 2012; Ogutu et al., 2014), and it is possible that restricted access of wildlife to permanent water sources has contributed to recent population declines in Kenya (de Leeuw et al., 2001). Some studies suggest this is because livestock and human activity around watering points prevents wildlife from sharing the resource (du Toit et al., 2017). For example, de Leeuw et al., (2001) found that high livestock densities near permanent water sources caused wildlife to concentrate further away. However, other studies suggest livestock and wildlife can spatially partition watering points on a broader scale; when cattle are concentrated further from permanent water bodies, water-dependent wild grazers can remain closer (Sitters et al., 2009). A less-studied aspect of coexistence is whether wildlife and livestock temporally partition water resources. A single study by Mizutani et al., (2012) reported that cattle and wild grazers utilised the same watering point over a 38-hour observation period, suggesting it is possible, but also noting that not all wildlife species showed temporal partitioning. Further studies to improve our understanding of the role of temporal partitioning in wildlife–livestock landscapes are necessary.

Here, we investigate whether wildlife (including carnivores) and livestock share the same water points in a dry season grazing refuge in the South Rift Valley, Kenya. We placed camera traps at known watering points along a perennial river, capturing images in two periods: first, when nearby settlements were unoccupied, and second, as people and their herds moved into the area seasonally. With this data, we measured wildlife presence and the difference in temporal overlap between livestock and wildlife activity at watering points. We expected temporal partitioning between livestock and wildlife to increase, with wildlife using water resources more at night.

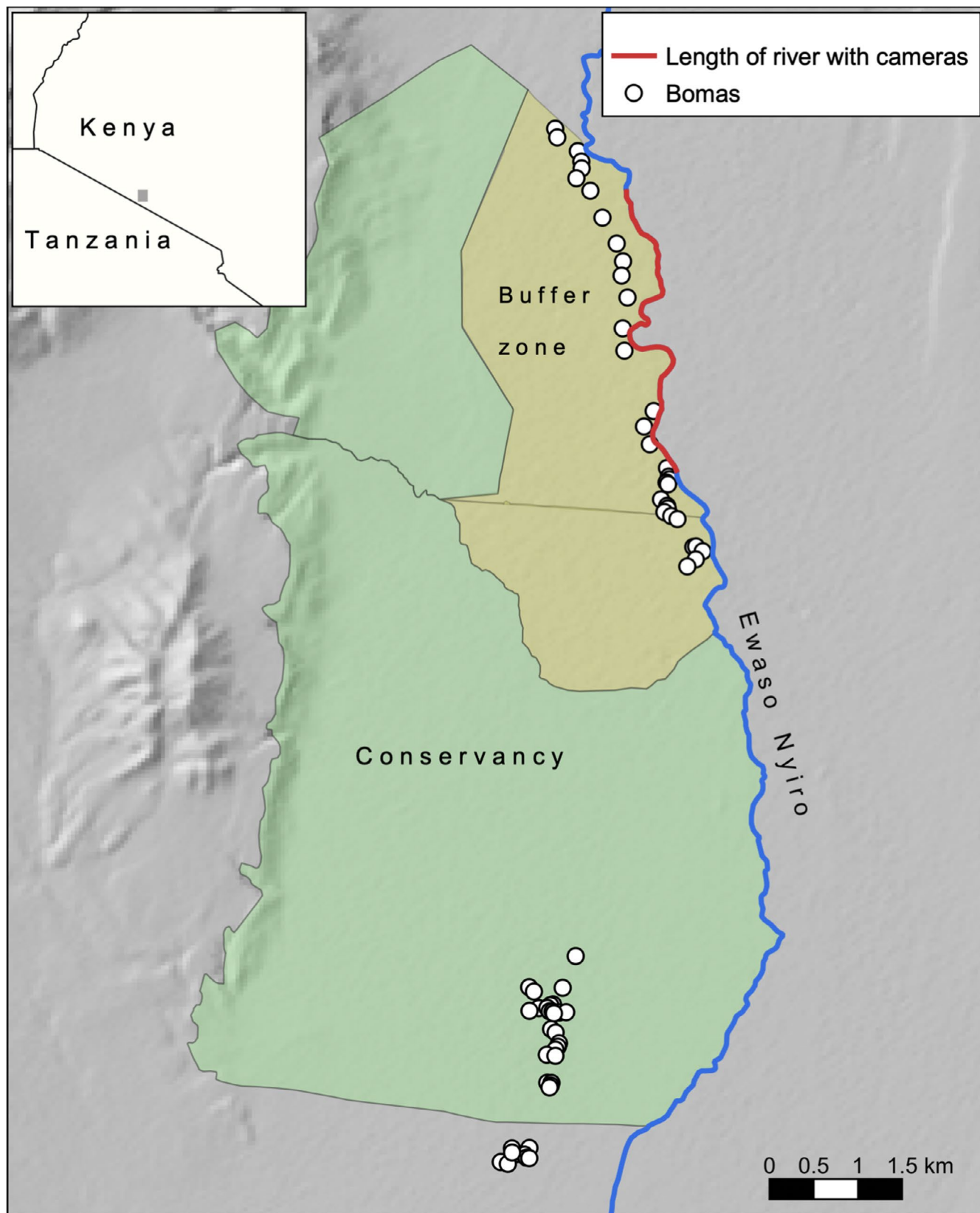
## 2 | METHODS

### 2.1 | Study area

The study area is located in the Southern Rift Valley of Kenya, with an altitude of 600–700 m and high temperatures ranging from 18°C at night to 45°C during the day. The area is semi-arid rangeland receiving low annual rainfall of 400–600 mm, which is bimodal and highly erratic with a percentage variability of 35% (Agnew et al., 2000; Schuette et al., 2013). Except for one perennial river, low rainfall combined with high evapotranspiration rates results in limited standing water available in the dry season (Russell et al., 2018). This study was conducted along the Ewaso Nyiro, the only substantial and perennial river running in the area. The Ewaso Nyiro flows into Shompole swamp and then into Lake Natron, providing an important source of water, particularly outside of the rainy season (Figure 1).

The study area falls within the Shompole and Olkiramatian group ranches, which together cover approximately 1000 km<sup>2</sup> (Russell et al., 2018). A group ranch is a land parcel owned collectively by its customary occupants (Fox, 2018; Kimani & Pickard, 1998). Approximately 20,000 Maasai pastoralists and their livestock inhabit this land (Agnew et al., 2000), alongside an intact herbivore community (except for black rhinoceros (*Diceros bicornis*)) and 21 species of carnivore (Russell et al., 2018; Schuette et al., 2013).

In this study region, the Maasai practice traditional seasonal movements, following grazing resources through three different land use zones: livestock rearing area, buffer zone, and conservancy (Tyrrell et al., 2017). During the wet season, livestock grazing is contained within the livestock rearing area (April–June), where settlement is permitted year-round (Tyrrell et al., 2017). As the dry season begins, settlements move into the buffer zone, from where the livestock can walk into the conservancy to graze, which is allowed only in the dry season (Tyrrell et al., 2017; Western, 2018). In this ecosystem, sheep and goats are often managed collectively while decisions regarding the movement of cattle are independent of sheep and goats (shoats); for example, cattle are moved into the conservancy before shoats, as per the conservancy grazing plan (Western, 2018). Additionally, herders accompany livestock during the day, so an increase in livestock presence is associated with an increase in human presence (Tyrrell et al., 2017).



**FIGURE 1** Map of the study area, showing all occupied bomas at the end of Period 2. Created with QGIS 3.10. GPS locations for individual camera trap sites are located in Table A1

## 2.2 | Boma occupancy and periods

Seasonal classifications are based on grass biomass and greenness; in 2013, June was considered wet and October considered dry (Russell et al., 2018). This study was performed during the wet to dry season transition, spanning July to September of 2013. During this time, Maasai herders moved into temporary seasonal settlements in the buffer zone near the river (Figure 1), allowing their livestock access to grazing and water resources in the conservancy. Period 1 ran from 25th July to 8th August, during which time only three bomas in the buffer zone were occupied. By the end of Period 2, which ran 19th August to 4th September, 65 bomas were occupied by the river in the buffer zone, with some bomas within 150 metres of the river (Figure 1). Although Periods 1 and 2 are relatively short (15 and 17 days, respectively), the change in boma occupancy between them is very large, resulting in large increases in local livestock and human populations. Additionally, these shorter periods ensure the study is not impacted by seasonal changes in forage resources which could influence wildlife abundance regardless of human pressures.

## 2.3 | Camera trapping

We set ten camera traps at ten major water points on the Ewaso Nyiro, spanning approximately 8.5 km of the river along the buffer zone (Figure 1). All cameras used were the Bushnell Trophy Cam 8MP with infrared flash. Depending on the natural vegetation available, each camera was set up roughly 10 m from the water point (range 5–15 m) and 0.5–1 m from the ground. The water points were spread relatively evenly along the river and chosen based on local knowledge of where livestock and wildlife use the river, which is limited to certain points due to steep banks (Table A1). The cameras were deployed in two periods of 15 and 17 days, respectively, from July to September. In the first period, Period 1, nine out of ten cameras operated perfectly, while in the second, Period 2, only five cameras captured images. Camera operation matrices can be found in the Appendices (Figure A1). Despite fewer functioning cameras in Period 2, we utilised data from all working cameras in both periods for all analyses, because habitat, human presence and distance to water were almost identical for each camera location within each temporal period throughout the study site (Hunter et al., 2020; Russell et al., 2018; Tyrrell et al., 2017).

## 2.4 | Camera trap data handling

Images were sorted and tagged in DigiKam version 6.1.0, and meta-data extracted with ExifTool version 11.35. Duplicate records were removed, and a five-minute independence criterion was applied to condense temporally dependent images into a single detection event (Niedballa et al., 2019). The threshold of five minutes was determined an appropriate length of time to cover one watering hole

visit by a species. Our camera traps did capture images of people ('human bycatch'). There is currently no widely followed protocol for handling camera trap images containing humans (Sandbrook et al., 2018). Images containing only humans were removed, and images containing both humans and livestock were classified under the appropriate livestock species only. In this area, livestock are always accompanied by people, so increased livestock presence also indicates increased human presence. To protect privacy, these images were not shared or published, and people were not identified. Members of the Shompole and Olkiramatian communities were made aware of the study taking place.

The complete detection record contains 1082 images of 11 species of interest (livestock and wildlife species potentially involved in conflict or competition) across 32 days. The literature surrounding camera trap sample sizes is conflicting, but Lashley et al., (2018) reported consistent results down to a sample size of 10 when investigating the full day activity of their species of interest. We deem a sample size of 10 or larger to be acceptable for our analyses, particularly because we are interested not in the overall amount of all-day activity between the species, but rather just when they are using key water resources.

We therefore analyse zebra ( $n = 135$ , 113 in Periods 1 and 2, respectively) and wildebeest ( $n = 23$ , 29) individually, in addition to the categories 'All wildlife' (all herbivore and carnivore wildlife species) and 'All carnivores' (spotted hyaena and lion) (Table 1). Because this ecosystem is metabolically dominated by zebra and wildebeest, trends in these species are crucial and accurately reflect impacts on the herbivore community (Russell et al., 2018). The category 'all wildlife' consists of baboon (*Papio anubis*), giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*), wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), spotted hyaena (*Crocuta crocuta*) and lion (*Panthera leo*). While the combined carnivore sample size is sufficient in Period 1 ( $n = 13$ ), it lies just below the threshold of 10 captures in Period 2 ( $n = 7$ ); we still present our results because these trends are relevant to both livestock management and conflict prevention. Livestock were split into individual species because in this study area they are managed independently; cows may drink at different times and graze in different areas than shoats.

## 2.5 | Species capture rates

All analyses were performed in R version 3.5.1 (R Core Team, 2017).

Species capture rates were calculated as number of independent captures per working hour taken across all working cameras, presented in Table 1.

Generalised linear models (GLMs) were constructed in R. Poisson's regression models with an offset (of the number of days cameras were active) were used to measure the difference in capture rates for each livestock and wildlife species between Periods 1 and 2. Camera station was included as a random effect to account for autocorrelation from repeated sightings at individual stations.



Species	Period 1		Period 2	
	Capture rate (captures per hour)	<i>n</i>	Capture rate (captures per hour)	<i>n</i>
wildebeest ( <i>Connochaetes taurinus</i> )	0.007	23	0.0141	29
zebra ( <i>Equus burchelli</i> )	0.0411	135	0.0547	113
cow ( <i>Bos indicus</i> )	0.0566	186	0.0998	206
domestic dog ( <i>Canis lupus familiaris</i> )	0.0043	14	0.0073	15
donkey ( <i>Equus africanus asinus</i> )	0.0319	105	0.0184	38
shoats (sheep and goats) ( <i>Ovis aries</i> and <i>Capra aegagrus hircus</i> )	0.0219	72	0.0281	58
All carnivores (spotted hyaena ( <i>Crocuta crocuta</i> ) and lion ( <i>Panthera leo</i> ))	0.004	13	0.0034	7
All wildlife	0.0684	225	0.0819	169
All livestock	0.1147	377	0.1536	317

TABLE 1 Summary of wildlife and livestock capture rates in Periods 1 and 2

Note: Capture rates measured in number of captures per hour across all working cameras. The category 'all wildlife' consists of baboon (*Papio anubis*), giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*), wildebeest, zebra, spotted hyaena and lion. The category 'all carnivores' consists of spotted hyaena and lion, and 'all livestock' consists of cow, dog, donkey and shoats (a collective term for sheep and goats as they are difficult to distinguish in mixed herds and are therefore treated together).

The Poisson regression was used because it is a robust model for count data, and the offset allows modelling of rates, rather than raw counts, which was necessary to account for the difference in camera trapping effort between Periods 1 and 2.

## 2.6 | Species activity patterns

Each individual species' drinking activity was plotted as a kernel density estimation for each species using the 'camtrapR' package in R (Niedballa et al., 2019). To investigate whether wildlife species activity at water points shifted temporally from Period 1 to 2, we ran Wald tests on drinking activity using the 'activity' package in R (Rowcliffe, 2019). Additionally, we measured the temporal overlap in activity from Period 1 to 2 for zebra, wildebeest, all wildlife and all carnivores (species groups with high sample sizes) using the 'overlap' package, to detect the directionality of any temporal shift in species activity patterns from Period 1 to 2 (Meredith & Ridout, 2018). Temporal overlap from Period 1 to 2 was quantified with  $\hat{\Delta}_1$  (Dhat1), a nonparametric estimator of the coefficient of overlapping, using the 'overlap' package (Meredith & Ridout, 2018). The overlap coefficient ( $\hat{\Delta}_1$ ) ranges from 0 (no temporal overlap in activity) to 1 (complete temporal overlap). 95% confidence intervals were then calculated for each overlap coefficient ( $\hat{\Delta}_1$ ) value from bootstrap estimates, using the 'overlap' package (Meredith & Ridout, 2018).

## 2.7 | Estimating temporal overlap

To estimate the temporal overlap in drinking activity between livestock and wildlife, activity was plotted as a kernel density estimation

for each livestock and wildlife species using the 'camtrapR' package in R (Niedballa et al., 2019). Activity for each wildlife species was then compared with each livestock species, and temporal overlap between each pairing was quantified with  $\hat{\Delta}_1$  (Dhat1), a nonparametric estimator of the coefficient of overlapping, using the 'overlap' package (Meredith & Ridout, 2016).

To further validate the overlap analyses, we ran a beta-regression using the 'betareg' package (Cribari-Neto & Zeileis, 2020). We analysed the change in proportion of daytime captures from Period 1 to Period 2 for the four most common species: zebra, wildebeest, cattle and shoats. Daytime was defined as 6:30 AM to 6:30 PM, the approximate times of sunrise and sunset in the region, respectively. Additionally, we calculated the time from a livestock capture at a water point to the next wildlife capture (excluding baboons), to quantify the temporal displacement effect that livestock have on wildlife species and better understand the overlap in activity between the two.

## 3 | RESULTS

### 3.1 | Livestock and wildlife species capture rates

We found a marginal but non-significant increase in capture rates of all wildlife species combined (Table 1) with increased human settlement from Period 1 to Period 2 ( $p$ -value = 0.08, estimate = 0.23). Captures of all livestock species combined increased significantly from Period 1 to 2 by 0.93 captures per hour ( $p$ -value < 0.001, estimate = 0.49). There was a highly significant increase in cattle captures ( $p$ -value < 0.0001, estimate = 0.69), and a non-significant

increase in captures of dogs ( $p$ -value = 0.07, estimate = 0.89) and shoats ( $p$ -value = 0.16, estimate = 0.25). There was a non-significant decrease in donkey captures ( $p$ -value = 0.18, estimate = -0.34) (Figure 2).

From Period 1 to 2, both wildebeest and zebra significantly increased in capture rate (wildebeest:  $p$ -value = 0.04, estimate = 0.69; zebra:  $p$ -value < 0.0001, estimate = 0.70). There was also a small, non-significant increase in captures of all carnivores combined (lions and spotted hyaena) (Figure 2).

### 3.2 | Species activity patterns

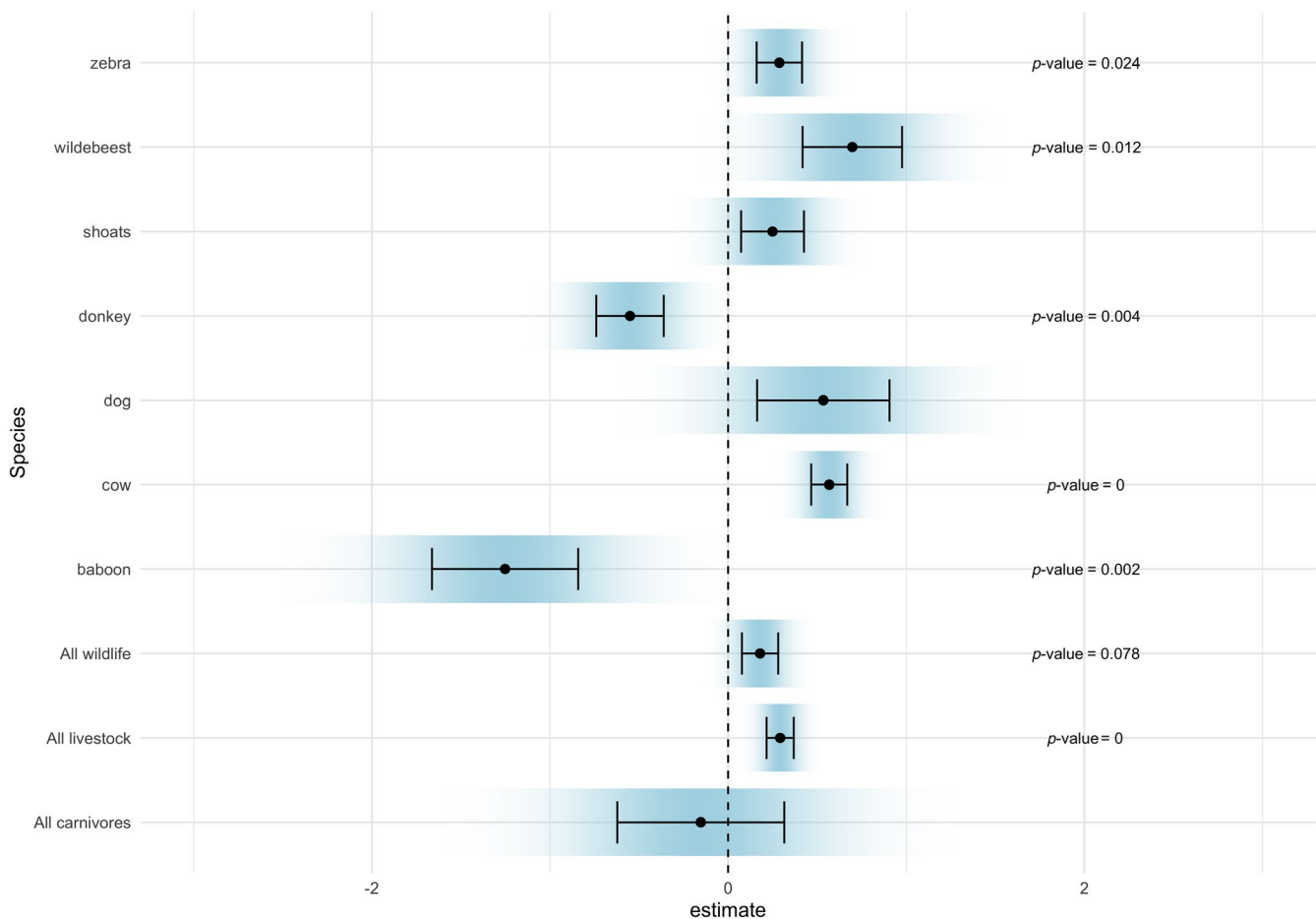
Our results from the Wald tests indicate that the activity patterns of all wildlife combined did shift temporally between periods, which was a near-significant effect (difference = 0.10, Wald statistic = 3.78,  $p$ -value = 0.052) (Table 2). The within-species overlap analyses show that there is both increased night-time activity and considerable aversion to daylight drinking in Period 2 for each wildlife species individually and combined, indicating that the shift in

activity detected by the Wald tests is towards increased overnight water use (Figure 3). Overlap values and confidence intervals are located in Table A2.

### 3.3 | Temporal overlap

Overall, temporal overlap between livestock and wildlife at watering points decreased with increased human and livestock presence, from Period 1 (nearby bomas unoccupied) to Period 2 (nearby bomas occupied). All species pairs show a decrease in temporal overlap from Period 1 to Period 2, with wildlife detected more at night while livestock visit watering points more during the day (Figure 4). Some species pairs have non-overlapping confidence intervals, showing significant differences from Period 1 to 2, including cow and wildebeest, livestock and all wildlife, livestock and carnivores (Figure 5). Overlap values and confidence intervals are located in Table A3.

Our beta-regression analysis indicates that of the four most commonly captured species (zebra, wildebeest, cows and shoats),

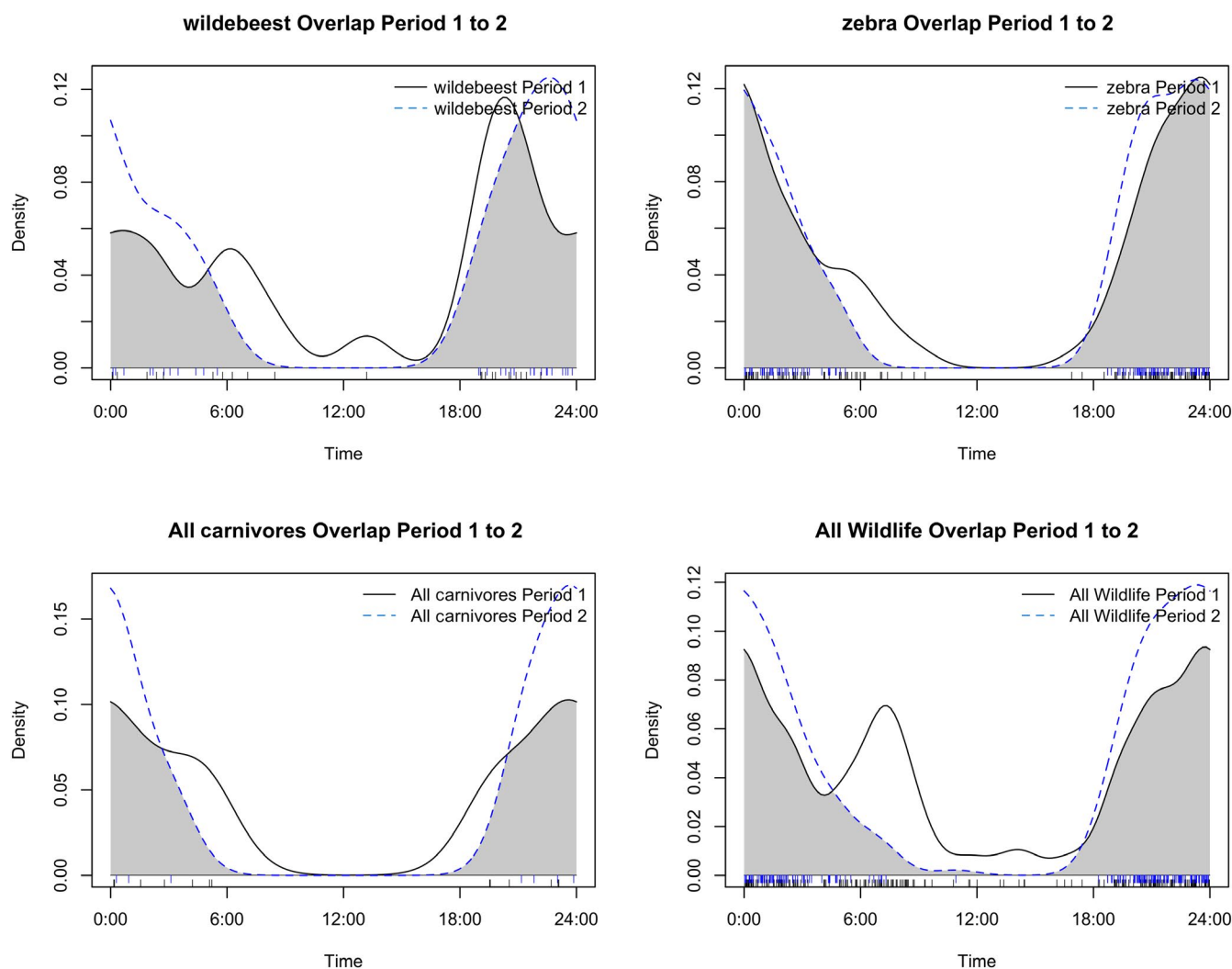


**FIGURE 2** Difference in capture rates (captures per hour) of wildlife and livestock species from Period 1 (nearby bomas unoccupied) to 2 (nearby bomas occupied), plotted with 95% confidence intervals (blue gradient) and standard errors (error bar). 'All wildlife' includes baboon, impala, giraffe, wildebeest, zebra, spotted hyaena and lion; 'All carnivores' includes spotted hyaena and lion. Left of the dotted line indicates a decrease in capture rate and right an increase.  $p$ -Values omitted when  $p$ -value > 0.1

Species	Difference between estimates	SE	Wald statistic	p-value
wildebeest	0.0243	0.1076	0.051	0.8214
zebra	-0.0029	0.0453	0.0041	0.9492
All carnivores	0.1605	0.0948	2.8647	0.0905
All wildlife	0.1042	0.0536	3.7808	0.0518

**TABLE 2** Statistical outputs from Wald tests for each species

Note: Differences between estimates represent change in water point activity from Period 1 to Period 2.



**FIGURE 3** Overlap in individual species activity patterns at water points from Period 1 (nearby bomas unoccupied) to 2 (nearby bomas occupied). Each species' activity shift indicates increased daylight avoidance of water in favour of higher night-time activity

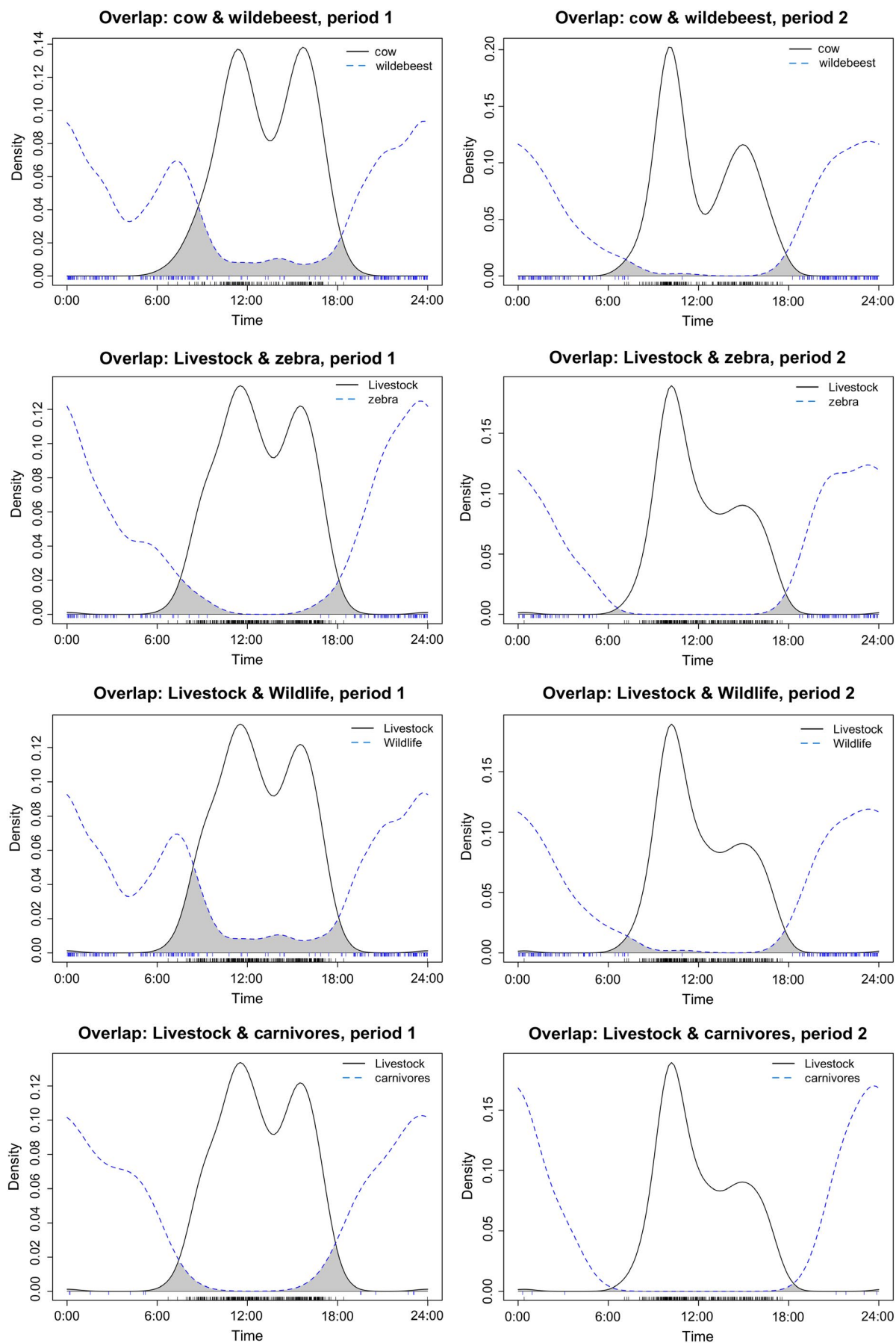
the proportion of daytime captures from Period 1 to Period 2 decreased only for wildlife species: zebra (significant,  $p$ -value < 0.01) and wildebeest (not significant,  $p$ -value = 0.20). There were no captures of zebra or wildebeest during daytime in Period 2. Full output is located in Table A4. Additionally, we found that the minimum time between a livestock and wildlife species using the same water point was 1.08 hours, with a mean time gap of 9.58 hours and a median time gap of 8.90 hours.

## 4 | DISCUSSION

### 4.1 | Temporal partitioning facilitates spatial coexistence

We examined wildlife presence at water points before and after humans and livestock settled in bomas along the Ewaso Nyiro river, on pastoral community land in Kenya's Southern Rift Valley. Despite a





**FIGURE 4** Selected temporal overlap activity plots of interesting species groups with potential for conflict or competition interactions. In each pairing, temporal overlap in activity at watering points (denoted by shaded grey area) decreases significantly from Period 1 (nearby bomas unoccupied) to 2 (nearby bomas occupied). Note: y-axis scales vary per graph

significant increase in livestock activity at watering points, wildlife detections at these same points remained steady, with an overall marginal but statistically non-significant increase in captures for all wildlife combined, as well as significant increases in captures for wildebeest and zebra. This increase in wildlife captures is likely because as the dry season progresses, the Ewaso Nyiro becomes an increasingly important water source, being the only perennial river in the area (Russell et al., 2018). Livestock have been reported to prevent wildlife from accessing water resources (du Toit et al., 2017) and to displace wildlife species (de Leeuw et al., 2001; Sitters et al., 2009). However, our results suggest that livestock activity at watering points does not necessarily negatively affect the ability of wildlife to access water, when wildlife are able to access shared watering points at alternative times.

As humans and livestock occupied nearby settlements, the temporal overlap between livestock and all wildlife decreased significantly. Many individual species also showed significant decreases in temporal overlap. These decreases correlated with a temporal shift in wildlife activity, as species visited watering points more at night while livestock were corralled. While increased livestock activity did restrict wildlife access to water during the day, wildlife species did not appear restricted from water access overall because they shifted to increase intensity of overnight water use. Our results show spatial coexistence, enabled by a temporal shift in water access, rather than the displacement of wildlife by livestock found in previous studies (de Leeuw et al., 2001; Sitters et al., 2009). Neither study (de Leeuw et al., 2001; Sitters et al., 2009) mentions livestock being corralled overnight, and both use aerial count data from the daytime only, ignoring the fact that wildlife moves at night.

Exploring variation in temporal activity can also provide insights into temporal niche partitioning as well as the effects of humans on other species' behaviours and interactions (Frey et al., 2017). For example, Wang et al., (2015) examined the effects of human influence on predator temporal activity, finding that in areas of higher human use, predators showed decreased diurnal activities in favour of nocturnal ones. Instead of measuring wildlife activity at multiple sites with different levels of human influence (as in Wang et al., 2015), our study measured the change in wildlife activity patterns at the same sites during two periods of distinctly different human and livestock activity levels. This allowed us to observe shifts in wildlife activity over time around a consistent set of water points as livestock activity increased.

In a study conducted in the Lolldaiga Hills in Central Kenya, Mizutani et al., (2012) reported a level of temporal partitioning of an artificial watering point by cows and wildlife over 38 hours of observation. While buffalo and elephants visited the watering point only at night, showing temporal partitioning, zebra and impala still frequently used the resource during the day (Mizutani et al., 2012). Our results also display temporal partitioning, but we have presented a more complete temporal divide between multiple livestock and wildlife species, both herbivores and carnivores. By Period 2, when humans had occupied nearby bomas, all wildlife species largely avoided watering holes in the daytime, with

notable decreases in the proportion of daytime captures from Period 1 to 2 for wildebeest and zebra. We further demonstrate the temporal divide by measuring the time gap from a livestock capture to the next wildlife capture at a water point, showing clear avoidance of livestock by wildlife on a short temporal scale. In addition, our study took place over a much longer time period and under two different levels of livestock activity, allowing us to measure the change in temporal overlap as conditions changed. The decrease in temporal overlap we found results from a behavioural change in wildlife species, showing that wildlife species can adapt to enable coexistence with humans and livestock in a matter of weeks. It is important to note that long-term wildlife monitoring in the study area shows wildlife populations have remained relatively stable and resilient over many yearly cycles of human migration in and out of the area (Russell et al., 2018). This suggests that wildlife have not declined at the same magnitude as in other pastoral rangelands (Groom & Western, 2013; Ogutu et al., 2016), an effect which would not necessarily be recorded in the relatively short time span of this study.

Though shifting to night-time water use facilitates wildlife access to a shared resource and permits livestock-wildlife coexistence, there are potential costs to increased overnight resource use for wildlife. For herbivores, increased water use overnight to avoid humans and livestock may increase their vulnerability to nocturnal predators, necessitating higher levels of antipredator behaviour, including vigilance (Gaynor et al., 2018). Predators, also avoiding humans during the day, may shift their diets to focus on prey that are abundant at night, resulting in increased predation for those herbivores with increased night-time activity (Gaynor et al., 2018; Sonnichsen et al., 2013). These shifts in ecology can have potentially transformative effects on ecosystems (Gaynor et al., 2018). However, in this study area, human and livestock presence in the conservancy is only elevated during the dry season, so increased wildlife activity at watering points overnight may have a less disruptive and seasonal impact on ecosystem function.

While all wildlife decreased in temporal overlap with livestock at water points, the extent of the responses varied by species. The water-dependent grazers, zebra and wildebeest, showed changes in activity pattern, largely mitigating direct competition for water with livestock in the day and visiting more frequently at night. Under higher livestock densities (Period 2), some temporal overlap still occurred in the early morning and evening.

Combined, the two carnivore species (lion and spotted hyaena) also showed a significant decrease in temporal overlap with livestock and no overall change in capture rates. Even before livestock increased (in Period 1), both species displayed a general avoidance of water during the daytime, visiting only at night when livestock were corralled in bomas. This result is in line with the typical nocturnality of lions and spotted hyaenas. The little temporal overlap with livestock that did remain by Period 2 took place in the early morning and evening, suggesting that conflict is most likely to occur during these times. This is useful information for livestock management; if conflict with carnivores is prevalent, people can

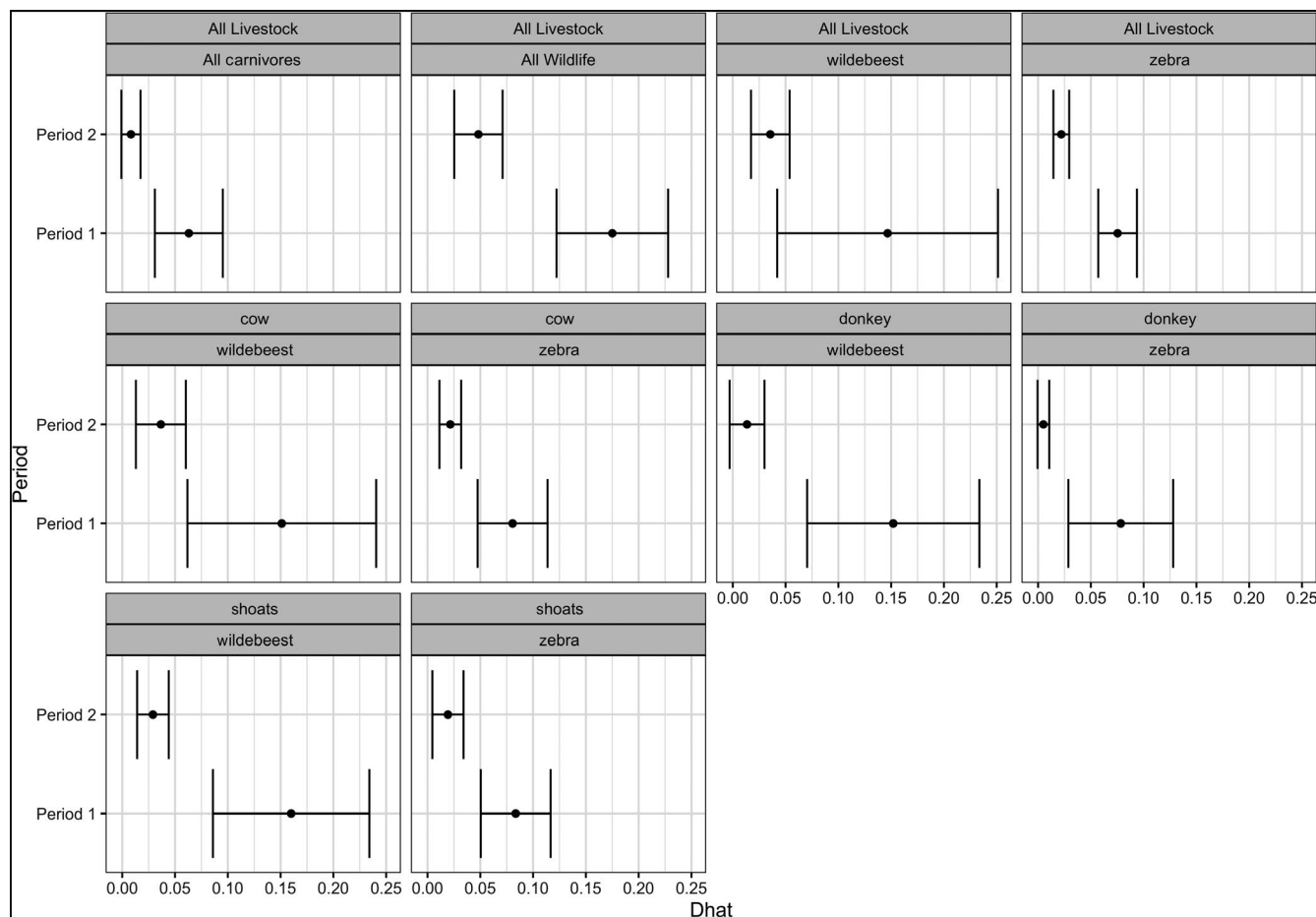
change their behaviour at these times to reduce temporal overlap and potentially avoid conflict. To expand on these results, a future study could investigate how wildlife respond to changes in livestock management practices, such as watering livestock earlier or later; wildlife species may respond by filling these temporal gaps in resource use.

## 4.2 | Cultural adaptations to coexistence

Adaptations by wildlife to access water more frequently at night are made possible by the Maasai practice of corralling livestock overnight. Keeping livestock in bomas is itself an adaptation to living in a coexistence landscape, its primary purpose being protection from predators (Western & Dunne, 1979). The use of bomas is not universal, but is a particular characteristic of many African rangelands. In rangelands with lower predator densities and smaller predator body sizes, such as in the midwestern USA, multi-paddock grazing is more popular, and cows remain there overnight (Provenza, 2003; Teague et al., 2013). A paddock is much larger and less protective than a boma, with enough room for the contained cows to graze for

a period of time. Without the danger of predation overnight, often because large carnivores have been removed from the landscape, livestock do not need to be so tightly corralled. Because livestock in paddocks are active both day and night, and are often spread homogeneously across a paddock, a multi-paddock enclosure near to a watering point may inhibit the ability for wildlife to utilise water points when compared to livestock kept each night within bomas. This is, of course, context- and scale-dependent regarding the underlying management systems. Thus, a larger enclosure in a rangeland with a lesser threat of predation may not allow for temporal partitioning of resources in the way that a boma does, instead resulting in spatial displacement of wildlife by livestock (Stewart et al., 2002).

Creating sufficient space for large herbivores and carnivores to access resources and complete large-scale migrations is a key goal in landscape conservation, and here, this is incidentally facilitated by herders acting in self-interest, protecting their livestock (Western et al., 2020). The presence of predator populations on the landscape therefore underpins human adaptation to coexistence with wildlife through the use of bomas, which then allows wild ungulates to adapt to coexistence with livestock. While nocturnal corralling may come at a cost to livestock production, potentially impeding livestock food



**FIGURE 5** Coefficient of overlapping ( $\hat{D}_{11}$ ) values plotted with 95% confidence intervals. Non-overlapping confidence intervals indicate a significant decrease in temporal overlap in the two species from Period 1 (nearby bomas unoccupied) to 2 (nearby bomas occupied). Dogs were removed because they almost always occur with humans and other livestock. Values listed in Table A3

intake and rate of growth, these mutual adaptations are necessary for livestock and wildlife to coexist (Carter & Linnell, 2016; Joblin, 1960).

Coexistence with wildlife often requires cultural tolerance (Western, 2018). In this context, tolerance is defined as passive acceptance—neither negative nor positive action taken towards wildlife (Bruskotter & Fulton, 2012; Western, 2018). The need for tolerance is most obvious regarding human and livestock interactions with predators (Legendijk & Gusset, 2008), but important also for wild ungulates. Because livestock and wild herbivores can compete directly over vital and sometimes scarce grazing and water resources (Odadi et al., 2011), coexistence brings associated risks and costs to livestock and people. For successful coexistence, local communities must tolerate these risks (Western, 2018). This tolerance is seen in Maasai livestock management decisions with no intention to affect wildlife negatively or positively, such as managed seasonal movements and the use of bomas at night. While there are both costs and benefits to coexistence, in this study, overnight corralling of livestock facilitates temporal partitioning, apparently mitigating competition over water resources, which in turn could lower costs of coexistence for people and wildlife sharing water points.

### 4.3 | Study limitations

While the complete data set used in this study was adequately large for our analysis (1082 records), some individual species had very few captures, preventing any specific conclusions from being drawn about their watering point activity. However, this did not impact the quality of our results, as species with lower sample sizes were easily aggregated into larger, ecologically similar groups, while the metabolically dominant grazers zebra and wildebeest were analysed individually. Because the movement pattern of these Maasai herders is seasonal, this study could be repeated for multiple years at the wet to dry season transition, generating the necessary repetition for sufficient sample sizes in each species. Adding more cameras at additional watering points would make the study more comprehensive, covering more of the river. Additionally, the study could be performed at the dry to wet season transition, to investigate whether wildlife resume more diurnal patterns of water resource use once livestock densities decrease. Movement into these bomas occurred over a few days, and while investigating the effects of individual bomas was not possible in this study, it could be considered in the future with more detailed occupancy data.

## 5 | CONCLUSIONS

Rangelands are globally important for both livestock and wildlife populations (Lund, 2007; Nicholson, 2000). Because large populations of Kenyan wildlife exist outside of nationally protected areas (Ogutu et al., 2016; Western et al., 2009), private and community-based conservancies play a critical role in conservation.

We show that livestock–wildlife coexistence is possible in a livestock-dominated pastoralist system and is facilitated by some

traditional livestock management practices. Wildlife activity at watering points remains stable through a period of rapidly increasing human and livestock settlement. Rather than experience spatial displacement due to increased livestock activity, wildlife species adapt to coexistence. Wildlife temporally shifts their behaviour, using water resources more at night, when livestock are confined in bomas. The use of bomas by herders is driven by self-interest, the need to protect livestock from predation, but incidentally creates space along the temporal niche for wildlife to access critical resources. Overall, temporal partitioning reduces contact rates between humans and their livestock and wildlife, potentially reducing risk of disease transmission, wildlife attacks on humans and human killings of wildlife (Gaynor et al., 2018).

While shifting to overnight water use permits access to shared water resources, wildlife may incur costs, including increased vulnerability to nocturnal predators necessitating a need for greater vigilance while drinking (Gaynor et al., 2018). Such consequences of coexistence for individual fitness, predator–prey interactions and potential ecological shifts warrant further investigation (Gaynor et al., 2018). However, wildlife populations have remained relatively resilient in our study area over years of human and livestock movement into and out of the conservancy, suggesting that increased wildlife nocturnality in the dry season has not significantly or permanently disrupted the ecosystem (Russell et al., 2018).

This study clearly shows the mutual adaptations by humans and wildlife necessary for coexistence. Humans adapt to coexistence with wildlife by protecting their livestock overnight in bomas. Wildlife species adapt to coexistence with humans and livestock by changing their activity patterns at watering holes to utilise the space opened for them at night. These co-adaptations to living in a shared system mitigate competition for a critical resource, water, and help facilitate coexistence among wild carnivores, wild ungulates and humans with domestic livestock. As wildlife numbers decline in Kenyan rangelands and livestock continue to form the basis of pastoralist livelihoods, understanding how to facilitate mutually beneficial land use solutions is increasingly necessary (Ogutu et al., 2016). This is especially relevant as OECMs with great potential to contribute to biodiversity targets (Dudley et al., 2018). Moreover, pastoral communities occupy huge areas of wildlife-rich land, so there is immense opportunity for community conservation to achieve large-scale impact and protection, and it is in the interest of national governments to support these initiatives (Kremen & Merenlender, 2018).

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### DATA AVAILABILITY STATEMENT

Data are available from the senior author on request.

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## APPENDIX 1

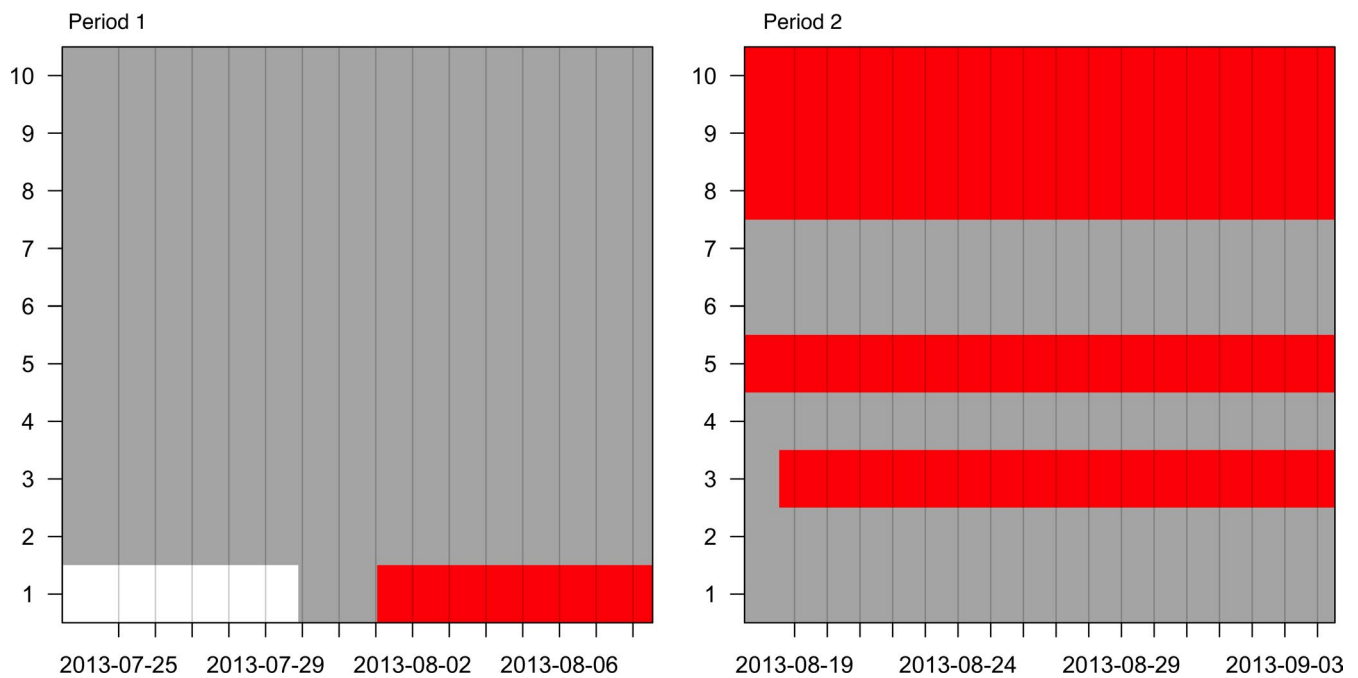


Figure A1 Camera trap operation matrices. Grey indicates a functioning camera, white indicates no camera mounted, and red indicates a malfunctioning camera

TABLE A1 GPS locations of camera trap stations

Station	Location
1	1°51'50.94"S, 36° 6'39.67"E
2	1°53'3.65"S, 36° 6'47.67"E
3	1°53'14.88"S, 36° 6'51.21"E
4	1°53'28.91"S, 36° 6'40.03"E
5	1°54'19.63"S, 36° 7'2.02"E
6	1°54'25.58"S, 36° 7'0.04"E
7	1°54'37.70"S, 36° 6'55.27"E
8	1°54'46.13"S, 36° 6'58.75"E
9	1°54'58.74"S, 36° 7'8.10"E
10	1°55'9.55"S, 36° 7'12.77"E

TABLE A2 Coefficient of overlapping values (Dhat) for individual wildlife species groups activity patterns from Period 1 to 2, with upper and lower bounds of 95% confidence intervals

Species	Dhat1	Lower	Upper	Period 1 n	Period 2 n
All carnivores	0.7274184	0.5206673	0.5206673	13	7
wildebeest	0.7424024	0.6238225	0.8609823	23	29
zebra	0.8884755	0.7905245	0.9864265	135	113
All Wildlife	0.7584219	0.6881572	0.8286867	225	169

TABLE A3 Coefficient of overlapping values (Dhat) for relevant species pairs in Periods 1 and 2, with upper and lower bounds of 95% confidence intervals

Species 1	Species 2	Period	Dhat1	Lower	Upper	Species 1 n	Species 2 n
cow	wildebeest	1	0.1511299	0.06172832	0.2405315	186	23
cow	wildebeest	2	0.03659251	0.0129279	0.06025712	206	29
cow	zebra	1	0.08059528	0.04747554	0.113715	186	135
cow	zebra	2	0.02158083	0.0112816	0.03188005	206	113
donkey	wildebeest	1	0.1520061	0.07043267	0.2335795	105	23
donkey	wildebeest	2	0.01349875	-0.0029944	0.0299919	38	29
donkey	zebra	1	0.07833853	0.02870281	0.1279742	105	135
donkey	zebra	2	0.00505517	-0.0004883	0.0105986	38	113
Livestock	wildebeest	1	0.146635	0.04205168	0.2512182	377	23
Livestock	wildebeest	2	0.03554234	0.01725184	0.05383284	317	29
Livestock	zebra	1	0.07534092	0.05702961	0.09365223	377	135
Livestock	zebra	2	0.0219975	0.0145043	0.02949069	317	113
Livestock	carnivores	1	0.0630914	0.09525005	0.03093274	377	13
Livestock	carnivores	2	0.00824906	0.01732255	-8.24E-04	317	7
Livestock	All Wildlife	1	0.1750656	0.2279119	0.1222192	377	225
Livestock	All Wildlife	2	0.048213	0.07110649	0.02531951	317	169
shoats	wildebeest	1	0.1600039	0.08592893	0.2340788	72	23
shoats	wildebeest	2	0.02907121	0.01409285	0.04404956	58	29
shoats	zebra	1	0.08354391	0.05045656	0.1166313	72	135
shoats	zebra	2	0.01935343	0.00459844	0.03410843	58	113

TABLE A4 Results of beta-regression analysis of change in proportion of daytime captures from Period 1 to Period 2. Performed on the four most commonly captured species

Species	Estimate	Std Error	Statistic	p-value
zebra	-0.6398	0.2454	-2.6074	0.0091
wildebeest	-0.6581	0.5126	-1.2838	0.1992
cows	0.5425	0.3924	1.3824	0.1668
shoats	0.3189	0.2742	1.1632	0.2448